UPLAND SOCIETIES OF PETOSKEY-WALLOON LAKE REGION

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 256

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(WITH ONE FIGURE)

Introduction

The writer became familiar with this region through spending the summers there for the past 12 years. During this time the rapid destruction of the few wild areas left suggested that studies be made while natural remnants were still available. The observations on which this paper is based have been carried on for at least three years. Besides the general data, 40 quadrats were made and a map of the plant geography (to be published later) was drawn.

The topography of this area was largely determined during the Pleistocene and Postglacial. LEVERETT and TAYLOR (**16, 17**) have covered this phase ably. At the time of the formation of Lake Chicago beaches this region was ice-bound, later forming part of the submersed area which gradually emerged as the waters changed from Lake Algonquin to the Nipissing Great Lakes, and through the Post-Nipissing stages to end in Lake Michigan. This periodic subsidence left the Algonquin, Nipissing, and later beaches (together with scattered morainal lakes inland), but erosion here has eaten away much of the Post-Nipissing levels.

The region at present is underlaid with Devonian deposits. Inland the surface layer is Upper Devonian, being largely black Antrim shale; while a marginal strip of about 3 km., from Petoskey west, and all territory north of the south margin of the Inland Route are covered with Middle Devonian. The latter contains the Petoskey limestone, which outcrops along the shore of Little Traverse Bay, either as shelving bedrock or limestone cliffs, the beds dipping inland. The lakes and channels have a layer of subaqueously deposited sand, covered in most places by black muck (fig. 1).

The region studied lies in Emmet and Charlevoix counties, Michigan. It includes a strip about 2 km. wide along Little Traverse Bay from Bay Shore to Idylwilde, together with Walloon

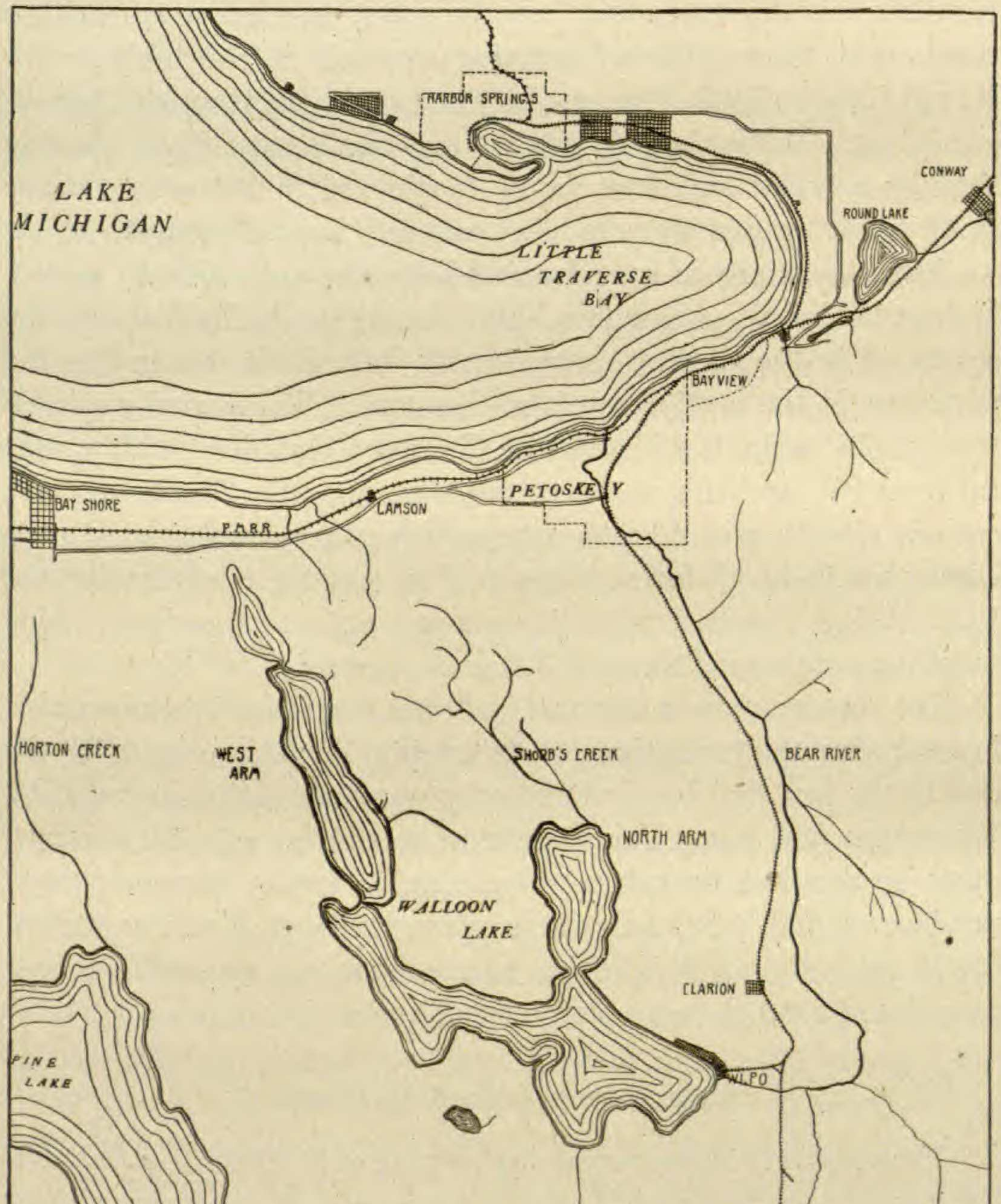

FIG. 1

Lake and surrounding shores. Bear Creek and Resort townships in Emmet County are also included.

The area of the region exceeds 260 sq. km. (about 100 sq. mi., of which about four remain in forest) and includes four upland masses, one between Pine and Walloon lakes, another between Bear Valley and Walloon Lake, a third between the latter and the Inland Route, and a fourth north of the Inland Route. Inland Route is a valley extending from Kegomic to Cheboygan, with a continuous water channel running through it, beginning with Round Lake on Little Traverse Bay and emptying through Cheboygan River. While the only river of any size is Bear River (flowing through a broad and deep valley northward to Petoskey), many small creeks empty into the lakes and into Lake Michigan.

The topography is irregular and hilly, the upland being mostly highest behind the Algonquin bluff, sloping gradually down to the southeast in the territory south of the Inland Route, and to the northeast in the portion north of the same. The varied glaciated topography suggests wide floristic diversity, combined with youthful form (**6**), and this is the actual state found. The region was entirely covered with forest before settlement; the uplands with the climax maple-beech forest of the region, and the channels like the Bear Valley, together with the swamps and creek valleys, being mostly a continuous stand of *Thuja occidentalis* L.

The classification of COWLES (**5, 6**) has been found more suitable in analyzing the formations of the region, but this may partly be due to the fact that less soil diversity was observed than found by WHITFORD (**25**) along Lake Superior, so that an edaphic arrangement seemed less desirable. The edaphic factor, however, could not be excluded, as in cases where one type of soil alone was studied (**9**, p. 46). COONS divides his successions into swamp (lagoon→forest) and sand (beach→pine barren) series (**20**, p. 60).

Upland types preceding climax

The upland societies remaining include only the late tree stages, the earlier ones being lost. For convenience of treatment similar areas in the older parts of other series will be discussed here. Three apparent stages are seen.

PINE FOREST

Only *Pinus Strobus* L. and *P. resinosa* Ait. occur. *P. Banksiana* Lam. has not been found, although it occurs around the south end of Lake Michigan, and in the pine barrens of northern Michigan as near as Wolverine in Cheboygan County. In general, the pine occurs in three places: (1) on the high hills back of Walloon Lake, (2) on Algonquin and Nipissing bluffs, and (3) as an early stage in dune forest succession.

The first location is a xerophytic open society of red pine sloping southward to the lake. The herbage below is dominated by ericads such as *Gaultheria procumbens* L. and *Vaccinium vacillans* Kalm. Occasional artificial clearings show an apparently succeeding stage whose components are crowded and mainly of shrub size. Here *Cornus* (*Baileyi ?*) and *Viburnum acerifolium* L. dominate. Following this is an obviously secondary society (may be absent in the primary series), taller than the preceding one and primarily *Betula alba* L. var. *papyrifera* Spach., with a mixture of *Populus grandidentata* Michx. and *P. tremuloides* Michx. Oak seems to follow.

The second type, almost entirely white pine, shows the oldest pines seen, growing on slopes approaching 45°, with sparse vegetation below characterized by *Solidago racemosa* Greene and *Shepherdia canadensis* Nutt. The xerophytic conditions here obtaining are indicated by leaves of *Aralia nudicaulis* L. 12 cm. across and 10 cm. tall, as well as by beds of *Polytrichum commune* L. Where cleared, the succeeding thickets are white birch with some *Prunus pennsylvanica* L. f. and *Amelanchier.*

The third type is a mixture of the two species, with white pine dominating, but with other conifers present. Among the particularly characteristic undershrubs occurring are *Corylus rostrata* Ait. and *Rosa acicularis* Lindl., while the herbage is largely of the ericoid type. At Menonaqua the full series is seen, but north of Harbor Springs erosion has eaten back into the pine society; the xerophytic conditions resulting permit persistence of much of the dune flora (telescoped succession).

As at present limited, pine occurs here near water in positions exposed to direct wind and of noticeably xerophytic nature. This agrees with its probable status as a relict tree formerly covering the upland. Transeau (24) believes conifers reached their present distribution in the lower peninsula of Michigan by way of the lake shores.

Oak forest

Quercus rubra L. furnishes an unimportant and rare type. Stands are seen near Walloon Lake, and on the Algonquin bluff north of Harbor Springs, which extend inland in places for some distance. This tree occupies the same sort of habitat as the pine, and probably succeeds the latter in certain areas. Oak also covers Harbor Point, a low Post-Nipissing area. The discontinuous distribution shown suggests relatively recent seeding at Walloon Lake. Along the bluff north of Harbor Springs oak succeeds pine, when trees of the former are near and the pines are far enough apart (or have been cut or burned off). This occurs especially where the slope is not steep. Invasion of the adjacent upland by oak has occurred in one place (5). *Quercus velutina* is absent from this region (13).

Hemlock forest

The few stands of *Tsuga canadensis* Carr. left are confined to areas similar to those bearing pine, but of less xerophytic nature. It appears that any area bearing hemlock in this region is ecologically prepared for the climax forest, for, aside from the fact that hemlock is more or less common in the climax forest itself, and that hemlock stands normally bear some deciduous trees, the undergrowth and seedlings of an open hemlock forest are usually deciduous, and where the trees are cut off the young growth is largely maple and beech. The periodic reproduction of conifers may have a disadvantageous influence on their persistence. On the low hills bordering Walloon Lake a nearly pure stand is common, running from an average of 20 cm. diameter to a maximum of 80 cm. In such a primary society few herbs or seedlings are scattered over the brown needle layer. The characteristic plants are *Taxus canadensis* Marsh, *Lycopodium lucidulum* Michx., *L. clavatum* L., *Clintonia borealis* Raf., and *Mitchella repens* L. Where cut off, the sapling flora is almost exclusively deciduous, being about 60 per cent *Acer saccharum* Marsh, mixed with *Fagus grandifolia* Ehr., *Acer pennsylvanicum* L., and *A. spicatum* Lam.

Beyond Menonaqua the pines adjoin a hemlock beech society, which very likely will succeed them. This represents the richest hemlock type seen, probably because farthest from the shore and most sheltered from the wind. The presence of many balsam and some oak seedlings, and the absence of sugar maple, make the next stage uncertain. Dense thickets of *Corylus rostrata* Ait. and much *Taxus* are characteristic. The hemlock on a Post-Nipissing level west of Harbor Springs is similar, but is mixed with *Abies balsamea* Mill. and *Thuja occidentalis* L. The Algonquin cliff west of Petoskey in several places bears large hemlock stumps of uniform (71–75 cm.) diameter, indicating that it was once largely occupied by a fine hemlock forest. The trees were cut sometime ago, for the secondary forest is nearly grown (average diameter 25 cm.), being beech, sugar maple, and *Betula lutea* Michx. f. A constant associate on open banks and cliffs is *Polytrichum commune* L., taking here as prominent a place as *Taxus canadensis* does in the level and denser part of the forest.

Climax forest

Seriation

The composition of the climax primary forest of the region has long been considered constant from the time the maple and beech reach dominance and respectable age. This is true floristically, but not ecologically or physiologically; for a climax formation is static in species, but dynamic as to individuals. Analysis of sufficient territory shows the forest to be more or less of a patchwork composed of trees in varying stages of development.

Cooper (4) found the climax forest he studied to be a "complex of windfall areas of differing ages, the youngest made up of dense clumps of small trees, and the oldest containing a few mature trees with little or no young growth beneath, those of a single group being approximately even-aged. This mosaic or patchwork changes kaleidoscopically through long time spaces, but the forest as a whole remains the same, changes in various parts balancing each other." His studies were of a coniferous forest. The climax here is deciduous, so differences are to be expected. The forest floor is lighter and the next generation starts sooner in the case of the maple-beech forest. The patches observed in the climax forest of this region are too large to consider as the result of one tree fall. Further, they would all have to approach the oblong or elongate form, whereas they are irregular where discernible, for the maple-beech forest is not to be considered as either patches of cleanly distinct even-aged trees, or as continuous forest with each generation even-aged throughout. It rather varies between these two ideals as limits.

Since the seriation is of individuals, the climax is not final, but recurrent, and during the development of each rough area or patch certain ages are to be recognized, each with fairly definite form, height, and spacing. At any one locality they follow each other in regular order, two or more commonly superposed, and adjacent areas independent of each other.

Definition of these ages is attempted approximately as follows:

	Age	Average diameter	Average spacing	Average height	No. per 100 sq.m.
Seedling........	1	5 mm.	40 cm.	40 cm.	670
Sapling.........	2	2 cm.	65 cm.	4 m.	300
Young adult....	3	15 cm.	3 m.	10 m.	10
Adult..........	4	50 cm.	6 m.	30 m.	3
Old tree.......	5	65–85 cm.	8–20 m.	35–40 m.	1

Ecological life history.—The flowers and fruits of the climax forest are mostly inconspicuous. Undeveloped fertile seeds are always present, as is shown by the abundant germination in clearings. The latter also emphasizes light as a critical factor.

Since the forest determines the intensity, amount, and continuity of the light penetrating, the number of seedlings (age 1) and their distribution depend largely on the forest's age. Many seedlings die, but are easily replaced They seem rare, but in reality often average 7 per sq. m., forming a scattered layer 20–60 cm. in height. The typical seedling form shows a slender, often branched, stem. The leaves are loosely corymbed or in one or two horizontal layers. The oval foliage outline results from free lateral growth (perhaps also spread to catch maximum of light). Apparently most of them remain nearly stationary for years. The taller ones appear distorted and dying, as if starved for light, which seems to decrease approaching the base of the sapling foliage.

Removal of the old trees above (15) permits freer elongation of the saplings. The seedling stratum becomes better lighted and watered, due to recession of foliage above and roots below. More seedlings germinate to fill the gaps, and elongation results in the formation of a new sapling stand (age 2) as the trees above reach age 4. The sapling axis is long and straight, forks and side branches equaling the stem are rare, and the foliate part of the tree, although polygonal in cross-section, approaches a right cylinder. The lowest branches are dead twigs, the later ones are horizontal or angle up.

A fine close sapling stand is the culmination in percentage of volume occupied. As the size of a stand increases, the distances between its trees increase also, and it is believed that a law will here be found to control relation of diameter and spacing of trees. The sapling age shows maximum increase in size for given decrease in number per unit area, hence competition between trees of equal age is keenest here.

With removal of another generation the saplings elongate, but intensity of vertical growth decreases, for the relatively open spacing permits lateral growth and reapproach to the typical broad form shown by isolated trees in field and pasture. In passing from the second to the third age a transition in branch form is seen, from the filiform type of evanescent branch to the massive type of permanent branch characteristic of the adult. These originate far above the sapling tops and hence are developed later. Comparison of the young adult and sapling stages with regard to ratio of height to breadth suggests partial etiolation in the latter. All saplings with forked axes are eliminated, since no adults are seen with forks at sapling level. Naturally a biaxial shoot is at a disadvantage under active competition with those supporting but one.

With further thinning of population the adult stage (age 4) is reached. This is the true ecological climax. The maximum foliage display and culmination of vitality are seen here. A typical tree was studied, felled, and measured. There was no sign of lost branches or decay, all branches bearing a rich display of leaves in normal position. The trunk was clean, straight, and subcylindric, with the lowest branch 25.3 m. from the ground. The diameter basally was 53 cm. and the tree was 32.5 m. tall. The crown was oval, with 12 major branches. The duramen showed a central cavity 8 cm. wide at the base, with its cone point ending about 2 m. above ground. Because of this cavity the age could only be estimated by proportion; the tree was approximately 250 years old (allowing for thicker early rings).

The senile or last stage (age 5) is scattered, because definite spacing is lost. Many primary limbs are gone, adventitious branches along the trunk and on otherwise dead limbs and stubs taking up the work. The heartwood is largely rotted. The sawed-off stump of one very old tree showed a cross-diameter of 120 cm., but only a margin of 15 cm. around the outside was wood, the rest being hollow. The base, at or near ground level, is often inhabited by a colony of big ants, and the breaking point is normally at this place. A certain degree of pliability is still retained in ages 4 and 5. The latter are apt to sway widely in a wind, some creaking loudly also under the strain; yet the tree may stay thus at the verge of fall for years.

Approach of death is equally indicated by the crown where symmetry is lost by branch fall. The top of an old tree is always ragged. These trees attain the maximum of height and diameter. They represent a wider range of age, dimensions, and form than any other of the life stages, partly because of their liberty of freer development than the younger trees below.

The beech follows the maple in general, but it is stockier, broader, and shorter, reaching each age much more quickly. Its terminal bud is weaker, and the tree apex is often injured by falling trees, lightning, and other destructive agents, so that the nutrients go to several branches near the top. As a result it is strikingly deliquescent and rarely develops a bole over 15 m. in height below the branches.

STRATIFICATION

MAXIMUM COMPLEXITY.—Investigators in the tropics have noted 5–7 strata in the rain forest (21). These were primarily due to the leafing out of the various tree species at different levels. It has been assumed that little or no stratification occurred in the climax maple-beech forest, the belief being partly based on the poverty of tree species (but two or three important) and the far lower degree of luxuriance as compared with the tropical rain forest.

Lower forest.....	Soil stratum: here lie roots, youngest farthest up. Leaf stratum: thin crisp continuous layer. Herbage stratum: includes seedlings also (age 1).
Middle forest....	Sapling trunks: first really open stratum; shrubs here. Death stratum: layer of dead twigs below sapling foliage. Sapling synfolium: sapling foliage layer.
Upper forest.....	Tree trunk stratum: ample light first reached. Upper synfolium: broken zone of adult tree foliage.

The strata of any one generation are best shown and fullest developed at the sapling age. They are not so well formed in the seedling and are breaking down in ages 3 to 5. Only major layers are listed. For this reason the seedling synfolium is not accorded separate rank (although thicker than leaf stratum).

SYNFOLIUM.—The synfolium is the layer formed by leaves of trees of the same age. It is the result of photosynthetic need in crowded sessile individuals. It must be dealt with not only as compound, with the unit the foliage leaf, but also as a mass. The placing together of all the synthetic tissue of a group of trees is of serious ecological importance. The leaf placing, together with the crowding of the trees, makes the vertical section of an individual show a nearly rectangular foliage mass. The synfolium governs its depth by means of the light relation. It also controls the amount and composition of the herbage below. In the general discussion here given, the synfolium of the sapling is taken as type.

While the synfolium continually and gradually ascends as the trees grow (no sudden jumps), the history of the foliage layer shows characteristic stages. Since the seedlings are scattered, their foliage layer is discontinuous horizontally. It is very close to earth level and is but 20–40 cm. vertically. As the sapling age approaches, the small foliage masses fuse into a continuous layer, having a much greater vertical section, and both upper boundaries parallel, horizontal, and nearly flat. This is the ecologic climax of the synfolium; here it reaches its greatest definition and density. Most of the growth is strictly limited to the top at this age, but later ages show the maple in its true light as more typically a deliquescent tree.

At the sapling age the synfoliar depth (from its top to its bottom) is 3–4 m. As it recedes from the ground its upper surface becomes uneven and covered with the free cones of the young adults, while spaces creep up from below. These result because lateral growth is insufficient to maintain closure. Increased lateral spacing now permits increased lateral growth, one of the prime factors slowing vertical elongation. Approaching the adult stage (age 4) the layer breaks up into its component tree masses. This occurs by rifting (vertical or horizontal breaks due to tree or branch fall), the gaps becoming nearly unfillable at age 3, for closure is either by elongation of a younger tree or by lateral growth of the adjacent tree circle. This age is the first one free vertically and laterally.

A further step is the breaking up of a tree unit into foliage clumps, one or several to a branch. Finally, many of the oldest lose all primary foliage, the trunk and branches bearing scattered handfuls of leaves. This secondary foliage is borne on slender twigs developed from adventitious buds. Gradual fall of the last age destroys all semblance of a foliage stratum.

Recession occurs in two main ways (trunk elongation unimportant): by shedding of leaves and branches at the synfolium base (the synfolium is self-pruning during the growing season), and by apical growth, the stems adding new leaves and branches, thus extending the synfolium compass vertically. With increase of synfoliar distance (from ground) and rifting, the herbage layer receives increasingly stronger light; thus the tree seedlings are stimulated to more active growth and the illumination of the forest floor decreases again.

The sapling synfolium contrasts with the trunk strata above and below, in apparent space occupied, color, and opacity. The lighting of the trunk stratum above is much greater, and that of the dead branch layer much less, being composed of flat, thin, horizontal tissue plates. The synfolium seems to have the ideal structure and arrangement for maximum of surface, light absorption, synthetic efficiency, and carbon dioxide use, together with the minimum material, volume occupation, and transpiration. The apparent effect on the eye gives impressive display and exaggerated idea of solidly filled space. This effect is heightened on passing from the bright sunlight into the dense shade of the forest.

YAPP (**26**) makes some interesting observations on evaporation at different levels in an English marsh, and SHERFF (**22**) on an

American marsh, finding evaporation rate proportional to height above the soil. These suggest that data on the levels of the climax forest of this region would be significant. GATES (8) compares evaporation at the chamaephytic layer in different societies but not at different levels. He believes evaporation a result, not a cause, of succession.

ENVIRONMENT

Competition is affected by several influences: physical and chemical factors, parasites, and individuals of the same or an older generation. Scattered among the herbage are tree seedlings, many of them dead or dying. In fact the younger the group, the more die. No competition between seedlings occurs except as two are found within short radius of each other. The critical competition for them occurs with the older trees in the form of light interception (most important) from above and nutrient interception from below. Since the lifting of the light inhibition is very slow in terms of potential seedling growth, the plasticity of seedlings becomes a factor. Being so adaptable, one can fit itself to any rift by lateral growth; occasionally one with over 90 per cent of its leaves on a far side branch will be found. Maximum spatial crowding is reached in the sapling age, and consequently the most critical competition of the life cycle occurs here.

Approaching the climax of elimination, the first to go are those with too few leaves in the light. Among other causes this may be due to shortness, distortion, slow growth, or accentuated crowding. There are more weaklings and distorted trees at this age than at any other, and in their removal comes the critical stage in spacing evolution; for removal of the very old trees above results in intensified elongation and more rapid destruction, since the spacing interval is increased 20–100 times before the third life age is reached. In general, the sapling race is not only a struggle for life by vertical elongation, but it is one in which the time element is crucial.

Having reached the third age, the tree is nearly immune from lateral competition, the permanent stand being formed here. Future struggles are against rot, parasites, wind, and weather, both root and branch systems now being amply competent to maintain life processes. Since the tree's juniors must be limited to what it cannot use, survival remains with the soundest and best developed. The final picking off in ages 3 to 5 seems slight. In the last age the result of unequal battle with parasites comes out and all fall in turn. It is the rare exception that remains to the last age, one of 100,000 seedlings that have lived and died within its present sphere of influence (GLEASON). In the last age beech is largely replaced by maple in most localities, so that a pure maple-hemlock stand is found in places.

Seasonal periodicity is shown, for example, in the synfolium, present only during summer and part of spring and fall. Each fall it joins the preceding synfolia in the dead leaf layer, thus proving how little actual solid was in it. Chromatic periodicity is more accentuated than in Illinois. The synfolium is yellowish green in spring, quickly turning to the darker green retained through the summer. In fall the birches turn yellow and many maples scarlet. Growth periodicity is shown in the alternating periods of relatively slow growth and active elongation (especially of saplings), according as the inhibition of an older generation persists or is removed.

Evidences of dying or death are unobtrusive but ever present. Nature seems very wasteful in her development of adult trees. The number of saplings pinned down by débris is remarkable. Many are thus actively destroyed instead of passively dying for lack of light. It is needless death and destruction that should in large measure be eliminated by scientific forestry, thus obviating the waste of space and light taken to develop useless plants at the expense of those later useful. Below the sapling synfolium is a death layer which bears, aside from the trunks present, many dead and dying branches.

Branches do damage in proportion to their size, the culmination of destruction coming in the fall of an adult tree. Tree or branch fall is primarily caused by basal rotting. Wind, rain, or lightning is usually required to crack the last resistant marginal alburnum of a branch or unbalance the tree (which has a different type of balance from a branch, so that it can break through proportionally much more wood). The big tree rarely catches on others to remain propped for a while. It usually falls without warning, snatching off branches from its neighbors, and pinning down or lacerating hundreds of young trees and saplings. There is thus left a natural glade to be closed by regenerative succession.

Competition and parasitism are the main causes of death. Destruction of branches at the synfolium base by lack of light is due partly to slower growth, but primarily to disadvantageous position. In old trees the most serious causes of death are boring insects, fungus rot, loss of foliage and branches, and (possibly) decreased vascular efficiency.

The parasites present are mainly insects and fungi. Neither show prominently in the forest, remaining more or less hidden except for fungus sporophores and many adult insects. Forest floor pileate forms are characteristically present, but individually not very abundant. COONS (20) points out that fungi may also be grouped in formations, certain species being characteristic of each type of habitat. Conditions in the climax forest, especially of the lower levels, favor fungus growth by the relative twilight, more equable temperature, and higher humidity prevailing.

Tunneling bark beetles are present, and, because *Tilia americana* L. and *Fraxinus nigra* Marsh. seem more often attacked, the insects may aid in keeping maple and beech dominant. These beetles, being cambium eaters, would seem more destructive than the duramen eaters, such as *Tremex columba* of maple and beech.

Leaf parasites (23) seem rather few. *Rhytisma acerinum* forms black blotches on maple and oak leaves. A similar fungus causes scarlet patches. Mites causing bag formation on the upper surface of maple leaves, and plant lice occur persistently; woolly aphids (*Schizoneura*) blight the alder, but rarely injure the hardwoods; several sorts of leaf-eating *Microlepidoptera* are found that are worst on the birches, while the tent caterpillars (*Clisiocampa*) confine their attention almost exclusively to rosaceous trees. Thus the maple and beech would seem to enjoy relative immunity from the more serious pests, which may aid in their retaining dominance. The débris includes leaves, twigs, branches, trunks, and stumps, most being found on the ground. Arrest is rare for very light objects (leaves and twigs) and for heavy large ones (trees), but for different reasons. The numbers of the different sorts of débris vary inversely with their size. The leaf layer at the ground surface, furnishing protection and humus, is characteristic of the climax forest. Unlike conifer needles, the leaves fuse during the winter into a single tough layer averaging 2–5 mm. thick, thinnest in late summer and thickest in late fall. Its base continually decomposes, adding to the humus below.

Twigs are always abundant on the forest floor; and since the herbage is open they interfere little with it. Their fall is light and they reach the ground soon, being smooth and slender and not liable to catch. They are easily pushed aside by all plants. Branches often remain on the tree for some time after death, but combined action of basal rotting and weather eventually tears them loose. Yet even then one may not fall, at times hanging by a strand of cortex and alburnum that is often remarkably small, or it may catch on the parent or a nearby tree at one of the crotches or lower branches. Usually one large branch is found on every 3–10 sq. m. Annual vegetation can be hurt for but one season, but perennial aerial parts are injured permanently.

The fallen trunk rots slowly, leaving a soil ridge and a narrow lane for many years. Stumps rot as slowly into a low mound, but hemlocks remain standing as giant stubs 10–20 m. tall with the branches lost. Their wood rots until it cuts like putty, but the bark will hold up for many years, being thick and tough, rich in tannin, and not rotted by fungi or eaten by insects. Maples and beeches rarely leave such stubs, except as the result of fungus entrance some distance up the trunk. Those that are left do not stand long.

Lichens are found sparingly on trunks above the sapling synfolium and on exposed trees. They are also seen on the larger branches and are more common on the maples and hemlocks, because the beech affords poor foothold. A year after a big tree falls, however, its bark is covered by a luxuriant and varied growth of foliose lichens, in consonance with the removal of the substratum from a xerophytic to a richly mesophytic environment.

Mosses are not common on vertical trunks. Ferns are not seen as epiphytes in this region, though not from lack of either individuals or species. Both may be found growing on rotting stubs (not hemlock).

FLORISTICS

GATES (7) and COONS (20) define many of the societies found in the region discussed here. It is hoped in a later paper to point out the differences observed from the floristic types recorded and described by these authors (1, 19).

NORMAL TYPE.—This occupied practically all the uplands of the region before clearing. There are 70–90 per cent sugar maple, 5–30 per cent beech, and the hemlock is a constant tree also, running as high as 25 per cent in some localities. Since many of the forests are not strictly undisturbed and hemlock is taken first (for barking), a low percentage or absence of it may be thus explained in some instances. Other trees occur in varying but small proportions, among the more prominent being *Tilia americana* L., *Fraxinus nigra* Marsh, *Acer spicatum* Lam., *A. pennsylvanicum* L., *Ostrya virginiana* Koch, *Betula alba* L. var. *papyrifera* Spach, *Prunus pennsylvanica* L. f., *P. virginiana* L., *Betula lutea* Michx. f., *Acer rubrum* L., *Ulmus fulva* Michx., *U. americana* L., and *Staphylea trifolia* L.

As type of this forest a quadrat in the primary undisturbed forest back of Bay View was taken (500 sq. m. in 20 squares). There were 17 big trees here, averaging 47 cm. diameter, making the average area occupied 29 sq. m.; 8 of these being maple, 5 beech, and 4 hemlock, although the hemlock is more numerous than in much of the nearby woods. Below these trees was a fairly open stand of saplings, those over a meter in height numbering 649; of which 57.3 per cent were sugar maple, 30.1 per cent *Acer spicatum*, 6 per cent beech, the other trees present being *Acer pennsylvanicum*, *A. rubrum*, *Ulmus fulva*, and *Fraxinus nigra*. Their average diameter was found to be 1.41 cm.; the average number per square (25 sq. m.) was 32.5. In a square studied near Walloon Lake the number of saplings was 89 and the average diameter 1.9 cm. The larger size and number in the latter square were probably because it had no adult trees in or very near it, while the Bay View quadrat had, so that its saplings had received only part of the light and nutrients that would otherwise be available.

It will be noticed that *Acer pennsylvanicum* and *A. spicatum* are prominent at age 2 in the first quadrat, and also in some of the climax forest. This is a similar phenomenon, but more accentuated than the one observed by COOPER (4) in regard to the balsam on Isle Royale. These two maples are ecologically of the sapling type; that is, they reach their highest development in a form ecologically equal to the second life age of the sugar maple. Beyond maturity they have such a high death rate that, although often as abundant as sugar maple at the sapling age, they are rarely represented in the third age. GLEASON'S (11) significant tabulation shows *Acer pennsylvanicum* as the dominant tree after clearing. The contrary occurrence from that of the maple is observed in the case of the hemlock, very few seedlings of which are seen in the climax forest, although a fair number of the adults are constantly present; for, because of scattered occurrence of young trees, it is not probable that the species is dying out.

Shrubs are not common through the climax forest. *Cornus alternifolia* L. f. is often seen in the Bay View woods. The characteristic shrubs of the region include *Sambucus racemosa* L., *Ribes Cynosbati* L. (transitions to *R. gracile* Michx. seem to occur), *R. lacustre* Poir. (along Little Traverse Bay), *Lonicera* (*L. hirsuta* Eaton is occasional along Little Traverse Bay), *Taxus canadensis* Marsh, *Rubus Idaeus* L., *R. allegheniensis* Porter, and *Aralia racemosa* L. The last is really an herb, but it is so tall and large that it is ecologically a shrub and occupies the shrub stratum.

The herbage of the climax forest is varied and fairly abundant. The prevernal flora is sun-loving and close, forming continuous masses of foliage composed of few species and many individuals. In the upland woods the dominant species is *Dicentra canadensis* Walp., but in the woods along Little Traverse Bay *Dentaria diphylla* Michx. appears more prominent. Transition forms to the summer flora occur; for example, *Caulophyllum thalictroides* Michx. is prevernal in leafing and flowering, while in fruit it is strictly aestival. *Allium tricoccum* Ait. also has prevernal leaves which die down before the scape appears in early summer.

The summer herbage is more scattered and richer in species, its richness varying with the age of the youngest tree generation. It is shade tolerant, and characterized by about 50 species. Particularly characteristic among them are *Botrychium virginianum* Sw., *Aspidium spinulosum* Sw., *Trillium grandiflorum* Salisb., *Maianthe-*

mum canadense Desf., *Tiarella cordifolia* L., *Geranium Bicknelli* Britton, *Mitchella repens* L., and *Aralia nudicaulis* L. A typical (1 sq. m.) quadrat at Walloon Lake contained *Geranium* 10, *Viola canadensis* 10, *Allium* 9, *Osmorhiza Claytoni* 2, *Galium triflorum* 1, *Dentaria* 2, grass 2, *Botrychium* 1.

At Bay View the herbs and shrubs show something of a tendency to segregation into patches dominated by different types. Three quadrats of a square meter each taken here were: (1) *Tiarella* 92, *Streptopus roseus* 8, *Dentaria* 4; (2) *Taxus* 24, *Dentaria* 8; (3) *Allium* 116.

Variants.—Both xerarch and hydrarch types can be distinguished. The xerarch occurs on high or hilly ground and is both drier and more open. Either hemlock or beech is prominent. The hydrarch type, shown well behind Bay View, is found in valleys and low ground, either occurring along streams or bearing standing water part of the year. The characteristic trees are linden and yellow birch. The herbage is closed and rich, as many as 40 species being found. *Marchantia*, *Equisetum scirpoides* Michx., orchids such as *Listera convallarioides* Torr., *Impatiens biflora* Walt., *Viola canadensis* L., *Glyceria nervata* Trin., *Polygala paucifolia* Willd., *Habenaria* spp., and *Lycopus* spp. are common; but the most typical character is the large number of ferns. Among the more prominent are *Adiantum pedatum* L., *Asplenium angustifolium* Michx., *A. acrostichoides* Sw., *A. Filix-femina* Bernh., *Phegopteris Dryopteris* Fee, *P. polypodioides* Fee, and *Aspidium spinulosum* Sw.

Natural clearings.—Natural glades and openings occur throughout the primary forest. The fall of a tree is followed in a month or so by a rank herbage growth (11), not the fireweed-composite type often following lumbering, but largely composed of naturally native forest path and clearing species. Among these, by the second or third year, spring up suckers and seedlings of maple and beech, mixed with certain clearing tree species, which shade out much of the herbage growth in four to six years. In the healing of the forest gap the clearing trees may be prominent at first, but they are gradually replaced by the maple and beech in course of time. Among the clearing trees are *Prunus pennsylvanica* L., *P. virginiana* L., *Tilia americana* L., *Ostrya virginiana* Koch, *Ulmus fulva* Michx., *Fraxinus nigra* Marsh., and *Betula alba* L. var. *papyrifera* Spach. The herbage is of such species as *Aralia racemosa* L., *A. nudicaulis* L., *Dactylis glomerata* L., *Panicum* spp., *Ranunculus abortivus* L., *Solidago caesia* L., *S. canadensis* L., *Osmorhiza Claytoni* Clarke, and *Geranium Bicknelli* Britton. *Rubus idaeus* L. often plays a large part if the clearing is not too small and the seeds are introduced at a time when room is available.

Secondary scrub and interference

Terminology suggested (3, pp. 145–166)

1. Revegetation
   a) Primary: original or primary vegetation of the area.
   b) Secondary: vegetation coming up after removal of primary society.
      (1) Repetitive: secondary succession following course of primary.
      (2) Nonrepetitive: not following primary.
2. Degree of interference
   a) Partial: few adult trees felled.
   b) Incomplete: all adult trees felled.
   c) Complete: all but herbage removed.
   d) Destructive: all vegetation removed; includes areas where refuse is burned off.
3. Recurrence of interference
   a) Simple: occurs once; area left alone thereafter.
   b) Repeated: interim for partial recovery allowed.
   c) Continuous: repeated at short intervals so that no recovery is allowed.
4. Terrain: left clean, dirty (refuse left), or burned
5. Successional phases
   a) Regressive: reversion to an earlier stage, or "lower" floristic type.
   b) Delayed: same stage but individuals of an earlier age.
   c) Static: approximately same stage and life age.
   d) Progressive: succession hastened.
6. Ecological state
   a) Stage: as used for some point in succession of species.
   b) Age: as used for some point in succession of individuals.

Xerarch treeless societies

The upland herb and shrub floras appear to show five secondary societies.

Fireweed society.—Most of its species are not native. In clearings, particularly those resulting from destructive interference, with dirty or burned terrain, strongly regressive changes occur, especially where the soil is stirred up or the humus destroyed. It has been said (3, 9, 10) that this new association is not "lower" than a forest, since it is new, but regression can be conceived as meaning return to a stage where less use is made of the space and light available. Furthermore, forest will finally replace such a society, just as it blots out any naturally formed clearing. The change here is toward a physically and physiographically youthful aspect (rejuvenation of COWLES, 6). The surface soil gives the prevailing tone to the society, being gray or yellow, powdery, and nearly free of available water, radiating intense heat on a warm day.

Into this xerophytic habitat comes a clearing flora showing but a limited number of species, among which *Epilobium angustifolium* L. is dominant. Other species of importance are *Sisymbrium altissimum* L., *Erigeron canadensis* L., *Cirsium arvense* Scop., and *Verbascum Thapsus* L. Besides these occur also *Sisymbrium canescens* Nutt., *Lactuca scariola* L., *L. canadensis* L., *L. spicata* Hitch., *Ambrosia artemisiifolia* L., *Gnaphalium polycephalum* Michx., *Erechtites hieracifolia* Raf., *Sonchus asper* Hill., *S. arvensis* L., *Erigeron annuus* Pers., and *E. ramosus* BSP.

Most of these species have a profusion of wind-borne seeds, and they take possession by having seeds there, by resistance to harsh conditions, by rapid growth, and by seeding profusely over the area when once started, thus getting ahead of competitors. They are finally shaded out by saplings. Certain species of *Lactuca* were observed 3–4 m. tall, and while in "young" dry areas a society as scattered as in a desert may be found, in full development this flora can form a positively impenetrable jungle, particularly on hilly ground with a dirty terrain. Few societies in this region can show such a wide variation of form corresponding with as wide a range of environmental conditions.

THORN SOCIETY.—Its species are natives of the region. This society occurs much in natural clearings, but because artificial clearings and cutovers are so much more numerous in this region at present, the thorn flora is found mostly in such places. It is dominated first by *Rubus idaeus* L., which is commonly succeeded in turn by *R. allegheniensis* Porter. The latter can hold a patch for years against saplings when pickers are numerous enough to keep the trees down; but if the patch be undisturbed, the sapling growth can replace blackberry in a few years (pin cherry in 3 or 4 years). The thorn species are widely sown by animals that eat the fruits, so their armament serves rather for climbing and individual protection than for keeping out animals. *Erigeron canadensis* L. is the commonest holdover from the fireweed flora. Forerunner saplings are also very usually present. Thus this stage serves as transition where herb and tree meet. It can hold a vicinity far longer than the fireweed society.

FERN SOCIETY.—*Pteris aquilina* L. occurs with some grass on xerarch areas. Because of its flat-topped habit and proneness to form a pure stand of fronds of equal age and height, this fern forms a synfolium at from 40–80 cm. from the ground, the distance varying with age. Bracken is commonly associated with grass sod, coming in after continuous destructive interference in the drier hilly upland and exposed shore hills. Aspen often is found with it, both entering particularly after fire (12). *Myrica asplenifolia* societies of farther south (Little Manistee to Brethren) appear to be equivalent.

MILKWEED SOCIETY.—The species is not native of the region. *Asclepias syriaca* L., while common as a weed, and found in all sorts of societies, also forms a persistent, ubiquitous, and actively invading society of its own on drier upland and lowland areas. Like *Pteris*, it is often associated with grass turf, possibly because of the natural openness of the two societies. It probably enters after more severe and continuous interference than the bracken can endure. Because of its underground rhizome, xerophytic structure, tremendous reproduction, and efficient seed dispersal, it can maintain itself after continued cutting and even plowing. It probably would precede sumac in reclamation of unused upland pastures, and is prominent where interference (and turf?) prevents later successional stages in pasture and grassy upland.

SUMAC SOCIETY.—These species are probably native here. *Rhus typhina* L. and *R. glabra* L. occur in upland pastures, along roads, and in clearings, being primarily a bordering association (thus later than milkweed), occurring more often on closed (and especially clay) soil. It forms a stand 1–2 m. high, much opener than the milkweed, and being taller permits more herbage. Along roads it is often followed by maple-beech, although the regenerating climax forest can enter at any stage of the upland secondary series. One of the evidences suggesting equivalency of the thorn, fern, and milkweed societies is that sumac can follow any one, and that any of the three can succeed the fireweed flora.

Xerarch tree society

The aspen–white birch–pin cherry society varies much in general form and specific content, so three types (consocies) are found. The dominant trees are *Populus tremuloides* Michx., *P. grandidentata* Michx., *Betula alba papyrifera*, and *Prunus pennsylvanica* L.

Pin cherry–birch.—The birch may be absent. Pure pin cherry stands in particular occur in upland and middle level clearings following the thorn society. They can spring up suddenly. In spite of good light the lower branches remain slender and die early. The mode of growth is the arboreal expression of the clearing society type; all are also soft wooded. The pin cherry is ecologically peculiar in being strongly excurrent, with elongate form and filiform type of branches, wasting the minimum of tissue on laterals and trunk diameter. This gives it great power of vertical elongation, an aid in competition for place in clearings, but makes it short-lived; so in time it must give way to longer-lived hardwoods. Thus the forest of this type is fairly open, with good herbage.

Aspen–pin cherry.—This is a dry open xerarch type found along shore, especially on the ridge back of the Nipissing cliff. Often half the trees will be dead and the remainder equally divided between the two species. Herbage is scant or none, and dead twigs and branches are thick below. Such a stand is far opener than either maple-beech or cedar forest, although similar to the cedar in number of dead trees.

Aspen-Pteris.—This is found more on dry levels inland. The small-toothed aspen dominates (90 per cent or more); the large-toothed aspen is prominent; and some birch may be found. Being secondary, the herbage below the bracken synfolium suggests a high type of primary forest. The following species are found: *Gaultheria procumbens* L., *Cornus canadensis* L., *Lonicera hirsuta* Eat., *Corallorhiza* spp., and *Lycopodium tristachyum* Pursh. The bracken seems to interfere little with this herbage, in fact may protect it. They occupy a different level and seem complementary (22).

The preceding types are alternative. Which enters depends on soil conditions, topography, and seeds present. Aspen succeeds best after fire and in higher dry ground. Pin cherry seeds are bird-scattered (and fertile longer), thus being more apt to reach a favorable place. The xerarch tree society is able to enter in many cases where climax forest is sufficiently cleared, either with or without intervention of treeless stages. The greater the degree and the quicker the recurrence of interference, the more likely regressive changes are to occur, its amount and the environment determining whether the ensuing secondary state be repetitive or non-repetitive, and, if the latter, whether it be thrown back to tree, shrub, or herb stage (the farthest being the fireweed semi-desert), that is, the degree of rejuvenation.

Regeneration of the climax forest may be speedy, hardwood saplings following a mixture of fireweed and thorn. This results in a remarkable floristic mixture. Behind Bay View a nearly pure stand of red maple has been formed after cut over. At Walloon Lake the beech is apt to dominate in the regenerating climax forest. In other places *Acer spicatum* and *A. pennsylvanicum* are important. If the xerarch tree society takes charge of a district it may be followed by yellow birch and elm (18) before the climax supervenes. Grass turf may prevent tree entrance (11, 12), but it would appear that milkweed and sumac, at least for dry upland, could replace it.

Discussion

The upland societies here studied show that most of the area of this character was occupied before settlement by climax forest. The forest itself (as any climax) is static in species but dynamic as to individuals, so that the climax is not final but recurrent. Five life ages may be singled out in this forest, each with its own dimensions and ecological characters. Thus the sapling age shows maximum increase in size for given decrease in number per unit area, so that competition between trees of equal age is keenest here.

For the foliage layer is coined the name synfolium, and its development and ecological significance are analyzed. In connection with mortality, it is pointed out that very many saplings are pinned down by débris, and thus actively destroyed instead of passively dying.

The study of Kent County, Michigan, by LIVINGSTON (18) shows five societies, while the writer has distinguished four here. While this might be interpreted as meaning Kent County was not so far advanced, it must be remembered that: (1) oak and hickory play more important rôles in succession in the Grand Rapids area than at the north end of the southern peninsula; (2) LIVINGSTON recognizes three societies containing oak, and two with maple; in this region the four primary types tend to be mutually exclusive; (3) LIVINGSTON uses herbs as well as trees in definition of his societies, which the author has not felt justified in doing for this region as yet.

In examining the distribution of the secondary societies, it seems probable that the hypothesis laid down by LIVINGSTON holds in large measure, but it may be that this is only for societies enduring rather small differences in moisture retaining power of the soil; for the fireweed society (secondary) is able to endure a wide range in this particular, being shaded out, but not dried or drowned out.

Throughout this region the response of the plant societies to interference and changed environment has been adaptive, in so far as their constitution allowed. Some natural societies, such as the blackberry, are fitted to survive in partly wild areas. Others can invade the fields in competition with the crops. Characters required are quick entry, speed of vertical growth, quickness of fruiting after germination, quantity of seed production, and efficiency of distribution; for a given society may be here today and gone tomorrow, plowed under.

The best example of the weed type among the societies previously discussed is the fireweed society, which contains species that are being rigidly selected by man in his fight against them. These plants are likely to survive long after the maple-beech society is banished to the wood lot and city parkway; for evolution is toward the herbaceous annual type (as pointed out by SINNOTT and BAILEY in past evolution also), as best suited to the mobile environment furnished.

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OAK PARK, ILL.

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